NASA TECHNICAL TRANSLATION NASA TT F-15,521

PROJECTIONS OF THE AMPULLARY CRISTAE OF THE UTRICLE IN THE PRIMARY CENTERS OF THE VESTIBULE. MICROPHYSIOLOGICAL STUDY AND ANATOMOFUNCTIONAL CORRELATIONS

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Translation of "Projections des crêtes ampullaires et de l'utricule dans les noyaux vestibulaires primaires. Étude microphysiologique et corrélations anatomo-fonctionnelles", Brain Research, 44, 1972, pp. 337 - 355

NATIONAL AERONAUTICS AND SPACE ADMINISTRATION
WASHINGTON, D. C. 20546 APRIL 1974

PROJECTIONS OF THE AMPULLARY CRISTAE OF THE UTRICLE IN THE PRIMARY CENTERS OF THE VESTIBULE. MICROPHYSIOLOGICAL STUDY AND ANATOMOFUNCTIONAL CORRELATIONS*

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Introduction

Numerous studies have already been devoted to the activity /337*** caused in the vestibular centers by stimulation of the labyrinth receptors. Recently, even a microphysiological analysis of the lateral vestibular center of the cat has been done by Wilson et al. [23], then by Ito et al. [10], using the total electric stimulation of the vestibular nerve. In fact, the selective and comparative stimulation of the various reception areas of the labyrinth does not seem to have been attempted until today. The only exceptions are the heat stimulation of the semicircular canals in guinea pigs [5], and the various methods of rotatory stimulation in rabbits [6], and in cats [4]. The difficulties encountered by the investigator, in order to reach the various branches of the vestibular nerve, are apparently

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* Received for publication March 18, 1972.

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*** Numbers in the margin indicate pagination in the original foreign text.

sufficient reason for this. Problems of another nature have been encountered by anatomists. Most certainly, Lorente de Nó [12], in his classical study of the mouse, had already laid the basis of the vestibulotopia of primary centers. But the confirmation of this work, whether in the macaque [18] or in the cat [8], has required the localized destruction of the vestibular ganglion, since the selective preganglionic sections of the nerve proved to be without effect in the primary centers.

The present study, based upon the electric stimulation by means of short electric shocks of the different branches of the vestibular nerve, had as its purpose knowledge of the ways of projection of the different receptors, as well as the existence of a probable vestibulotopia in the lateral medial and descending vestibular centers. On the basis of the results obtained, we measured the diameters of the vestibular nerve fibers and registered the potentials at their level, in order to establish some anatomofunctional correlations.

Materials and Methods

(1) The recordings from 30 cats, anaesthetized with sodium pentobarbital with doses of 40 mg/kg injected intraperitoneally, /338 started 4 - 5 hours after the onset of anaesthesia. In some cases, it was necessary to use a complemental administration of barbiturate by intravenous injection, which was sometimes replaced by the administration of curare.

Surgical access to the different branches of the vestibular nerve was accomplished as follows: the head of the animal, placed in a tereotropic apparatus, was oriented so that the external semicircular canal was in a vertical position. By means of a dorso-caudal approach, it was possible, after opening of the "bulla tympani", to locate the fenestra rotunda. After removal of the external ear, the osseous arch delimiting the meatus auditorius externus, was carefully ground to reduce its thickness. The same thing was done to the facial canal in order to eliminate the seventh nerve. After this,

the promontory was abraded by means of a very small drill, until it was reduced to the state of a very fine osseous pellicle which could be easily eliminated. At this point, it was possible to detect under the operatory microscope, the utricular nerves with their macula, as well as the lateral and anterior nerves of the semicircular canals (Figure 1). Each nerve was hooked with two silver threads of 50 μm, at a distance of 0.5 mm, and carefully isolated except at their endings. They were finally cemented to the ear bar. These are the stimulation electrodes. In absolute value, the short shocks, used for the stimulation and with duration of 0.1 msec, had generally a voltage of 1.5 V, with an extreme value of between 0.8 and 3 V. From the physiological point of view, this maximum voltage represented twice the average threshold for the appearance of spikes (3 × N1). Under these conditions, when — during the same experiment — there was no response following stimulation of a branch of the vestibular nerve, the stimulus was considered ineffective. An additional proof of the stimuli selectivity will be given during the description of the results by the scarceness of the convergence phenomena.

Figure 1. Macrophotography of the peripheral branches of the vestibular nerve in the cat: ca — nerve of the ampulla of the anterior canal (upper); cl — nerve of the ampulla of the lateral canal (horizontal). It is possible to detect the origin of the membranous semicircular canals and the ampullary cristae. u — nerve of the utricular macula. 0.5 mm scale

The recording electrodes, in platinum or steel, had a resistance of 1 - 5 MΩ. The marking (calibration) on the point of the electrodes was done for the platinum electrode by electrolytic process, for the steel electrodes — by passing a current of 40 μA for 15 seconds (ferrocyanide method). The 40-μm-deep incisions, made at /339

the freezing point, were colored with cresyl violet. The reading was done by comparison with transversal and sagittal sections, obtained after imbedding in paraffin and alternately saturating with silver ammonia or dyeing with cresyl violet.

The neurophysiological information, fed to a computer, was sattistically analyzed.

(2) Two adult cats were perfused with a buffer solution of trioxymethylenephosphate at a pressure of 12 mm Hg, and of 7 mm Hg, during a period of 15 minutes each time [21]. The stato-acoustic nerve was removed under the operatory microscope, together with the ganglion and the ampullary and utricular cristae. The auditory and facial nerves were very carefully eliminated. The vestibular nerve was then immersed in a mixture of osmium tetroxide with a 2% phosphate buffer for two hours. After dehydration, it was imbedded in "araldite". Semi-fine slices, cut 1 μm thick with the Reichert ultramicrotome, were colored with toluidine blue. On one side, transverse sections were made along the normal direction of the postganglionic nerve fibers, and on the other side — following re-orientation of the same block — longitudinal cuts were made, including the ganglion and the receptors. This procedure made it possible to easily establish the correspondence between the transversally cut postganglionic fibers and the receptors. A series of pictures, with enlargement of 1000 and 830, respectively, was obtained with the two samples under study. On the first sample, the diameter of 2000 fibers was measured by perimetry of fasciculi taken at random. On the second sample, the external diameters of 6453 fibers, almost representing the totality of them, were measured by taking their smallest size. The statistical analysis involved the study of the shape characteristics (Pearson and Fischer coefficients), the comparison and adaptation (test of χ^2) of a normal law to the distribution given for the histograms of the ampullary and utricular fibers. The results were analyzed on a IBM 360.50. /340

A complemental physiological study was carried out with five cats, using an experimental procedure identical to the one adopted in part

one. The recording electrodes were made of a silver thread, 100 µm, with the reference being placed on the boundaries of the orbits.

Results

The results include a first part, dealing with the nature and the localization of the responses obtained in the primary centers. In the second part, the diameter of the vestibular fibers was measured, in order to facilitate the interpretation of the results obtained.

A. Physiological Study of the Responses in the Primary Centers

(I) Analytical study of the responses considered as a whole

In the three vestibular centers studied, 147 cells deprived of spontaneous activity were recorded, after stimulation of different vestibular branches. The responses obtained, preceded at times by a positive pre-synaptic potential which may include 2 components, particularly pronounced when the electrode has a weak resistance (Figure 2a), exhibit one, two, or several spikes which superimpose on slow potential N1 and N2. The latencies of all the first spikes, whether due to stimulation of the ampullary or utricular nerves, are grouped between 0.8 and 2 msec. The histogram of the latency periods shows two groups of responses: 66% are between 0.8 and 1.1 msec, while 34% show a latency between 1.1 and 2 msec (Figure 3). It is, therefore, possible to distinguish Type I responses with an average latency of 0.93 msec (± 0.01), and Type II responses with an average latency of 1.35 msec (± 0.03) (Figures 2b and c).

The majority of type I and type II (62%) responses exhibit one spike only. The other responses (38%) are followed by a second spike at 0.8 msec from the first one (double responses, Figure 3). In 28% of the cases, the spike follows type I response, and in only

10% of the cases — a type 2 response. This second spike appears with intensity of stimulation slightly higher than the preliminary intensity of the first spike, or 1.8 times the threshold of N1, and exhibits a definitely higher tendency to fatigue.

More infrequently, other types of responses appear, for example, in the form of successive spikes (Figure 2d). Considering their limited numerical importance, they have not been taken into account in the percentages previously given.

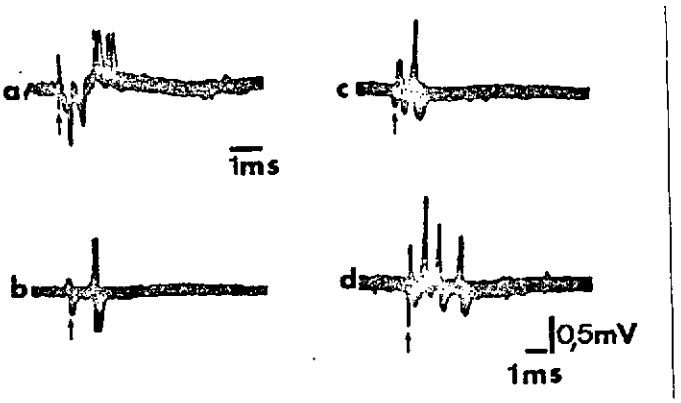

Figure 2. Electric stimulation of the vestibular nerve:

a, b — stimulation of the nerve of the lateral canal; c, d — stimulation of the utricular nerve. Each tracing refers to separate cells and includes 10 superimposed recordings. The arrows indicate the point of stimulation. a — recording with microelectrode of weak impedance showing positive prepotential with its two components; b — type 2 response: only one spike with long latency; c — type 1 response: only one spike with short latency; d — response including 3 successive spikes

(II) Characteristics of the responses as a function of the ways of stimulation

One of the objectives of our study was to look for a possible convergence of the impulses from the ampullary cristae and from the utricle on the neurons of the primary centers. Of the 147 cells studied in the three vestibular centers, 95 have been reliably tested, with at least two effective stimulations, only approximately 10 showing characteristics of convergence. We have compared the effects of alternate stimulation of the utricle and of a semicircular canal on 72 neurons. In this case, only 7 cells displayed a convergence of the two types of stimulation, while 31 cells responded only to the utricular stimulation, and 34 to one of the three ampullary

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stimulations. In those studies where only the stimulations of the nerves of the ampullary cristae could be compared, of the 23 cells tested, 4 exhibited a convergence of the impulses, 2 in response to the stimulation of the anterior and lateral canals, and 2 in response to the stimulation of the anterior and posterior canals. In the 11 cases of convergence, a receptor appeared always to be more efficient than the other, that is, the response to its stimulation had a shorter latency and formed very often successive spikes.

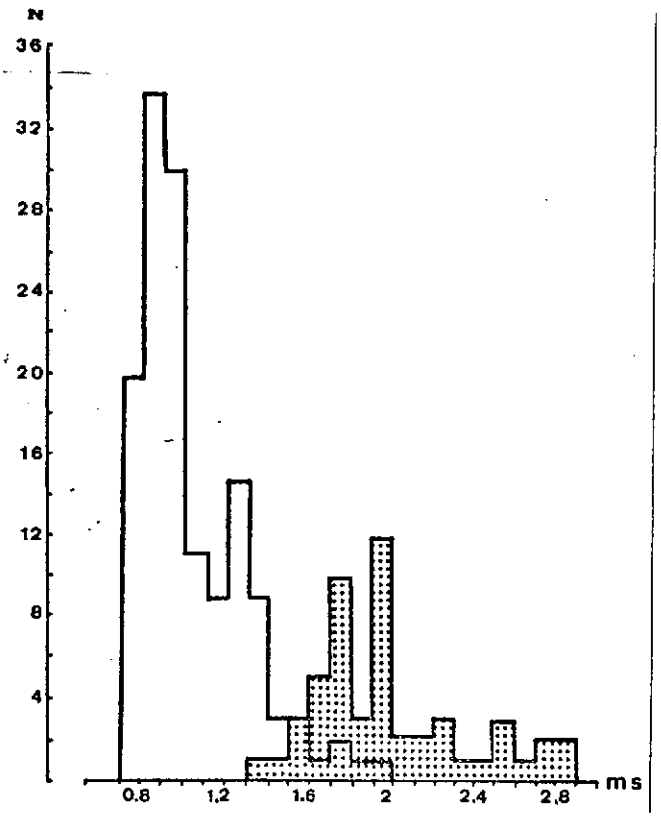

Figure 3. Histogram of the latencies of the responses recorded in the centers following electrical stimulation of the branches of the vestibular nerve. In white, latencies of all the first spikes (types 1 and 2); dotted — latencies of the second spike

If one compares the responses following stimulation of the utricle and the ones of the ampullae (Figure 4), it can be seen that there is a certain similarity in the reactivity of the vestibular neurons. In effect, one finds again the /342
different types of responses already described, and the proportion of double responses is the same (38%) no matter what receptor is being stimulated. There is, therefore, a considerable difference between the two categories of receptors. The responses brough about by the stimulation of the utricle have a latency superior to the one of responses obtained upon stimulation of the ampullae. It is for this reason that, among the variety of responses of type I, latencies as short as 0.8 msec are rare following stimulation of the utricle.

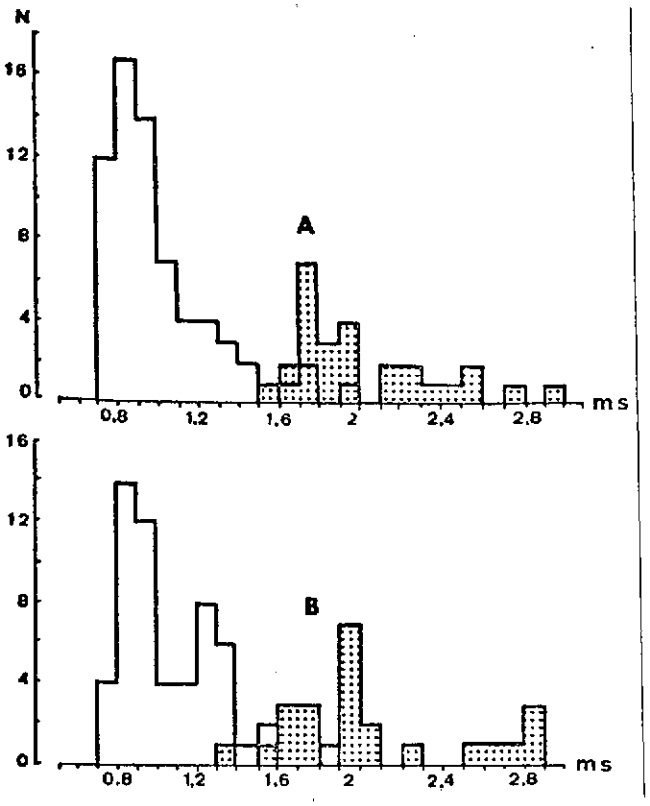

Figure 4 Comparison of the latencies of responses in the centers following electric stimulation of the different branches of the vestibular nerve. A — histogram of the latencies following stimulation of the nerve of the lateral canal; B — histogram of the latencies following stimulation of the utricular nerve. Notice, in this case, the importance of the first spike with long latency (type 2). The symbols used are the same as in Figure 3

Furthermore, type 2 responses are more numerous after stimulation of the utricle (39%) than after stimulation of the ampullary cristae (26%) (Figure 4).

(III) Characteristics of responses as function of their topography

The cells recorded are distributed in the three vestibular centers: lateral, medial, and descending (Figure 5). The responses to the stimulation of the fibers, in addition to the general characteristics described and summarized in Figure 6, exhibit different features, which will be examined later on.

(a) Lateral vestibular center. The majority of the 78 recorded cells are located in the ventral part, and their position as a function of the vestibular receptors shows a certain degree of organization: centro-medial for the ampullary cristae, and dorso-lateral for the utricle (Figure 5). The utricular projections are particularly important, since they represent 48% of the total. /343

The length of the latency of the utricular responses, which we have already mentioned, is very evident in this center. It is for this reason that 46% of the first responses have more than 1.1 msec of latency, while only 23% of this portion reaches this value

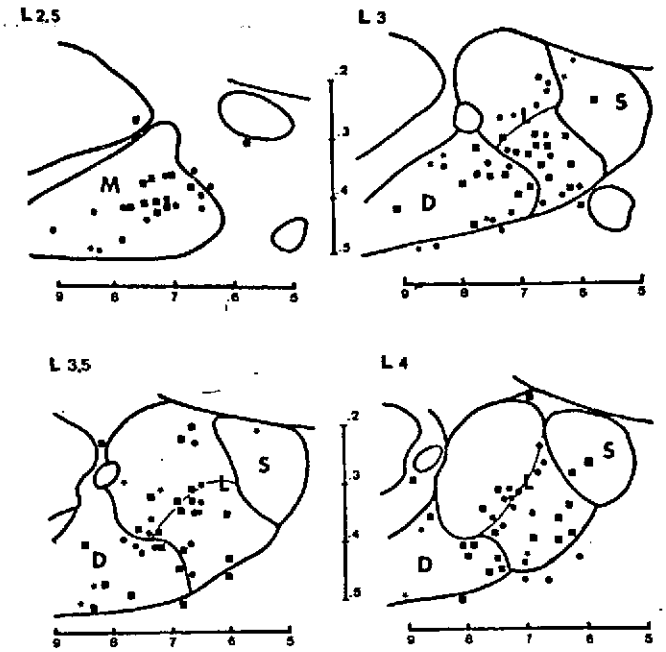

Figure 5. Organization anatomo-functional of the vestibular complex. Sagittal sections from plane L 2.5 to plane L 4 (personal coordinates):

M — medial center; D — descending center; L — lateral center (the dorsal portion and the ventral portion are separated by a fine line); S — higher center. Projection of the different receptors inside the centers has been represented by different symbols: * — posterior canal; ◉ — utricle; ■ — lateral and anterior canals

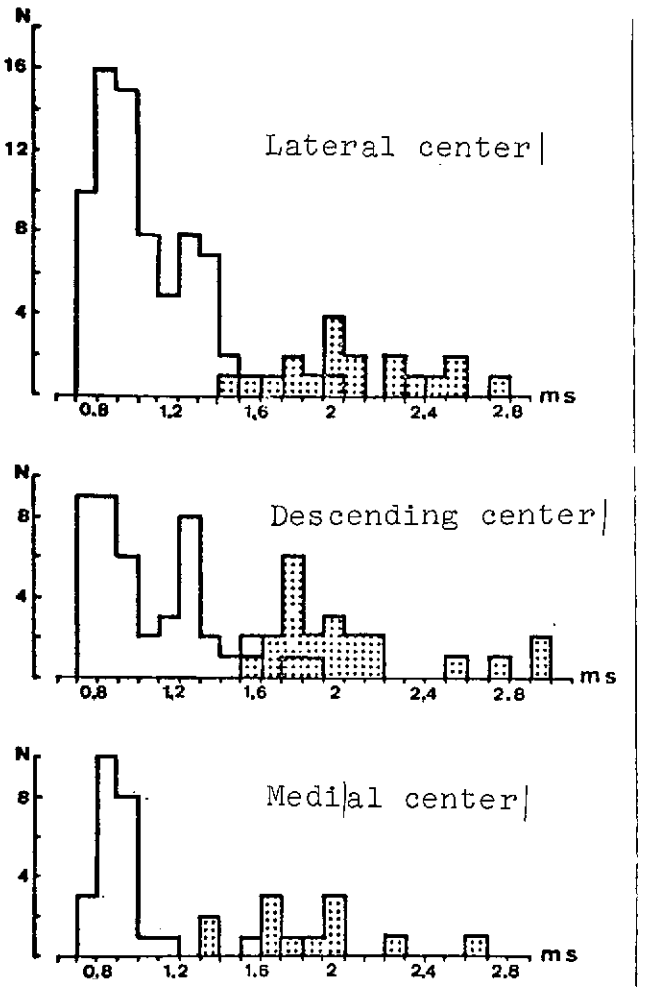

Figure 6. Histogram of latencies of responses of vestibular centers, lateral, descending, and medial. Notice the importance of the first spikes with long latency (type 2) in the lateral and descending centers. The symbols used are the same as in Figure 3

following stimulation of the lateral crista (Figure 7). As far as the double responses are concerned, their number (26%) is less than one half that encountered in the other two centers (Figure 6).

(b) Medial vestibular center. Twenty-five cells essentially located in the centro-rostral portion, have been recorded (Figure 5). If the stimulation of the ampullary cristae induces cellular

discharges, as one can expect, the same happens upon stimulation of the utricle. However, it seems risky to evaluate the respective importance of these projections, considering the small number of cells which have been recorded. It should be noticed that the proportion of the double responses is, in this type of structure, 50% (Figure 6).

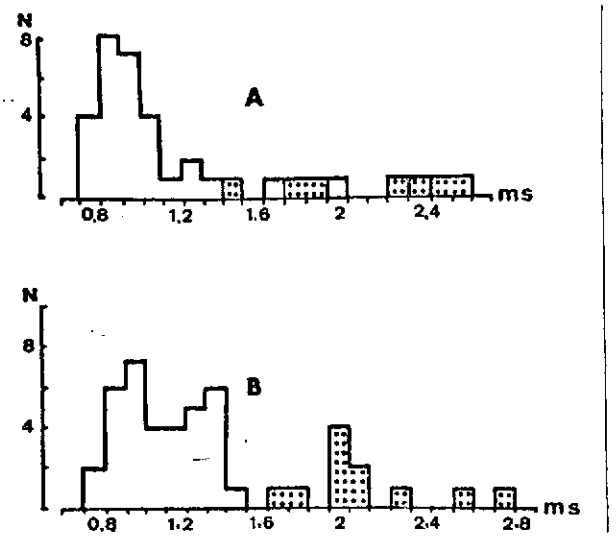

Figure 7. Histogram of latencies of responses in the lateral vestibular center. A — stimulation of the nerve of the ampulla of the lateral canal (33 cells); B — stimulation of the utricular nerve (35 cells). It is evident that the first responses located at more than 1.1 msec are due, for the most part to the utricular stimulation. Symbols used are the same as for Figure 3

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(c) Descending vestibular center. The 44 cells stimulated by the primary vestibular impulses are located in the rostral portion. The different receptors project themselves at this level without showing any vestibulotopia, while the histogram of latencies reminds of the lateral vestibular center (Figure 6). The number of double responses is particularly high in this center after stimulation of the ampullary cristae (60%).

B. Histological and Physiological Study of the Fibers of the Vestibular Nerve

(I) Histology

The spectra of the diameters of the fibers obtained by perimetry, or by measurement of the external diameter, show little difference. However, in the first case, the highest value for 1/10 of the fibers is 12.8 μm, while with the second method, the highest value attained is 10.2 μm. In spite of this, while the intermediary values are distributed in identical fashion, the direct measurement

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of the diameters was chosen because of its relative speed, which makes it possible to count almost all of the vestibular fibers (6453 fibers).

At the level of the internal meatus auditorius, the nerve includes a rostral portion, containing the fibers deriving from the ampullary cristae, and a caudal portion, containing the fibers deriving from the utricular and saccular maculae (Figure 8). We have isolated from our measurements the fibers located between these two parts surrounding the fasciculi of the efferent fibers. The diameter of 3217 fibers was measured in the rostral portion, and the one of 3236 fibers — in the caudal portion.

From the normal histograms of distribution (Figure 9), it appears that the diameters of the fibers in relation with the ampullary

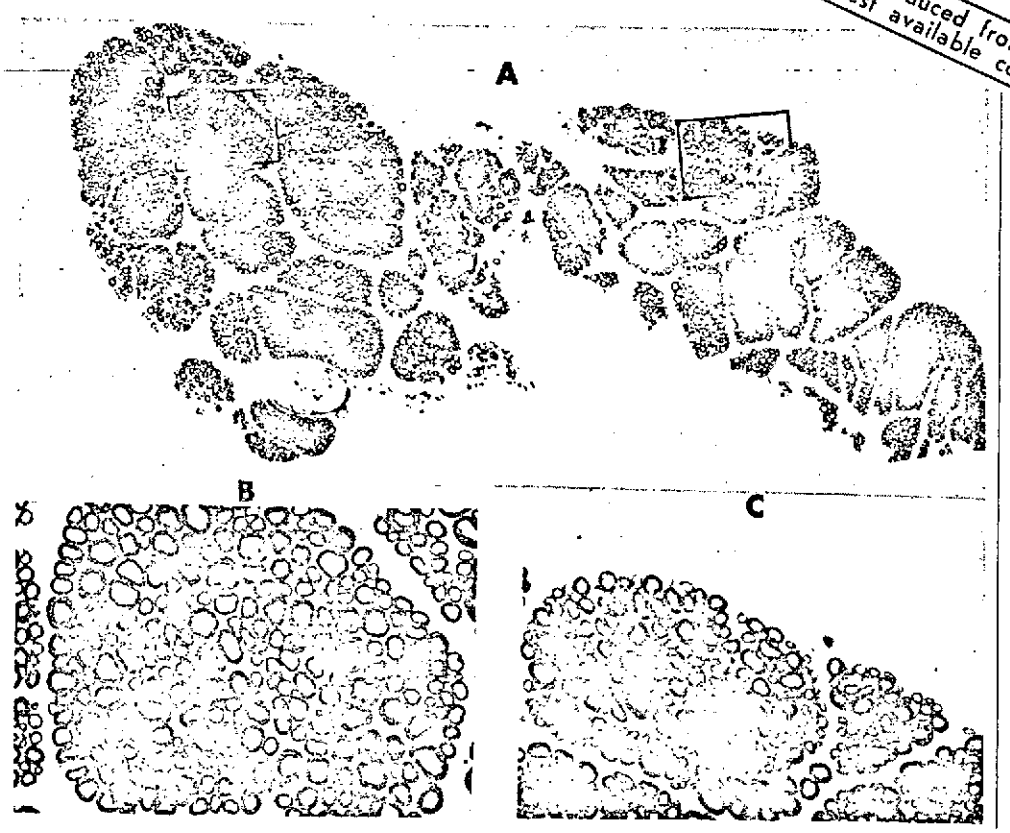

Figure 8. Transversal section of the vestibular nerve: A — total section (G × 185); B — detail of fibers of rostral portion (G × 580); C — detail of fibers of the caudal portion (G × 1290). Semi-fine sections. Toluidine blue

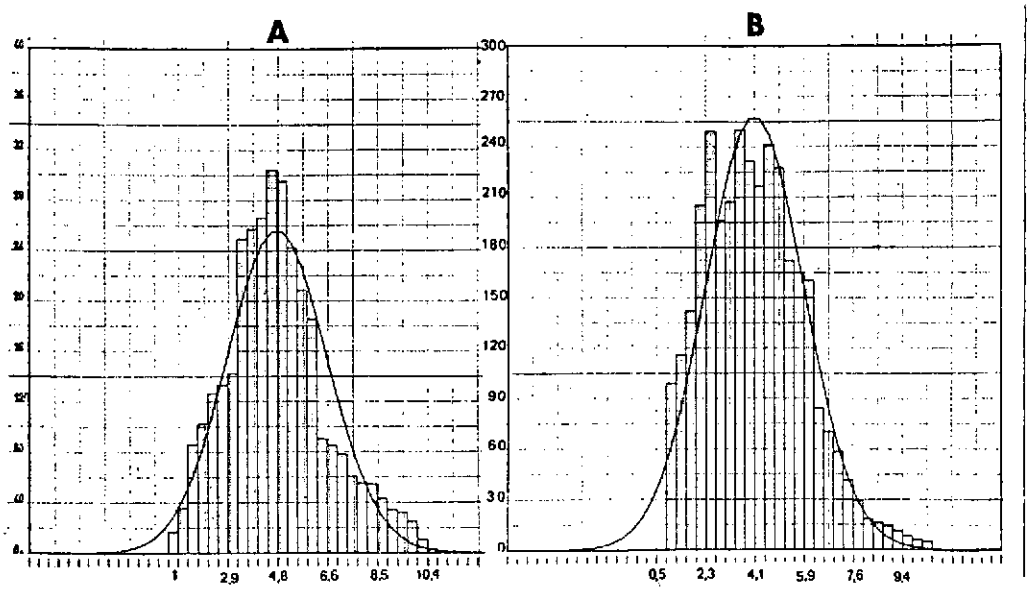

Figure 9. Histograms of diameters of the vestibular fibers. Comparison and adjustment of a normal law to the distribution of ampullary nerve fibers (A), and of the utricular and saccular fibers (B). Class interval: 1/5 deviation type: 1.87/5 for A; 1.80/5 for B

cristae do not obey a normal law, similarly to the fibers deriving from the utricular and saccular maculae. On comparison of the two populations, it appears very clearly that the ampullary fibers are significantly different from the utricular fibers and have a greater diameter (4.8 μm, as average, against 4.1 μm). Furthermore, from the point of view of distribution, the ampullary fibers have an almost symmetrical distribution around the average vlaue (S_1 = 0.007), while the utricular fibers have an asymmetrical distribution (S_1 = 0.28), spread more toward the higher values. For this reason, 58% of the utricular fibers have a diameter between 3.7 and 7.8 μm, and 39% of these have a diameter lower than 3.7 μm. For the ampullary fibers, these percentages are 70% and 23%, respectively.

(II) Physiology

The preganglionic electric stimulation of the ampullary and /347
utricular nerves being about, at the level of the intracerebral postganglionic fibers, action potentials having a double component

(Figure 10a and b). The detailed analysis of this component has been done by comparison with the histogram of the diameter of the vestibular fibers according to the method recommended by Bishop et al [1]. With this method, the histogram of the diameter of the vestibular fibers allows calculation of the action potential amplitude, as well as its shape, considering the fact that the product of the number of fibers and the cube of their diameter is proportional to the inverse of the diameter itself. The theoretical curves so obtained (Figures 10A, B) show various components directly related to the diameters of the fibers. Their comparison with the physiological recordings shows a very close correspondence.

In conclusion, if one studies the evolution of the components of the action potential as a function of the distance traveled by the nervous

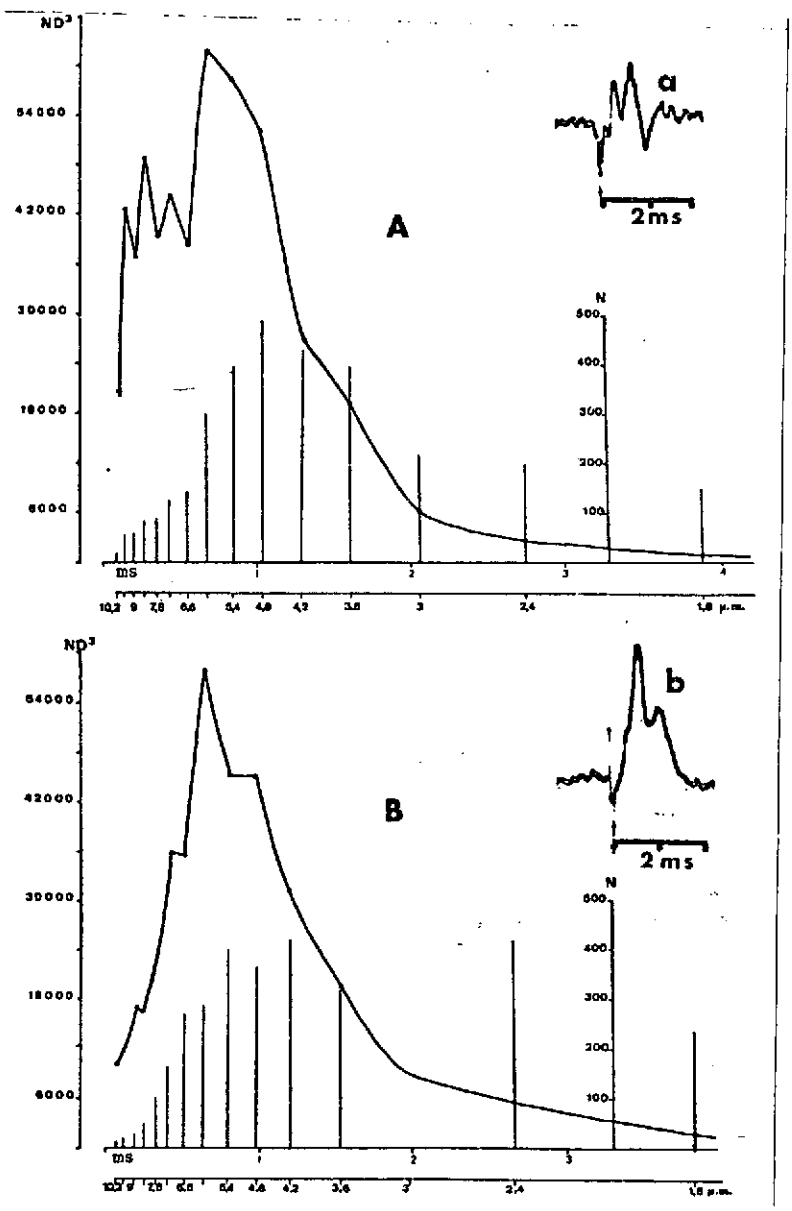

Figure 10. Reconstruction of the action potential of the vestibular nerve. A — potential of ampullary nerve; B — potential of utricular nerve. Vertical lines correspond to number of fibers grouped according to their diameter. Theoretical curve of action potential is obtained by plotting ND^3 on ordinate (where N is number of fibers; D — the diameter), and the inverse of the diameter on the abscissa. Scale for time intervals has been calculated as function of physiological recordings a and b, obtained with fasciculus of intracerebral vestibular fibers following stimulation of ampullary nerve (a) and utricular nerve (b)

impulse, it is possible to observe, following stimulation of the lateral ampullary nerve, that the shifting of the recording electrode of 0.5 to 0.5 mm, starting from the meatus auditorius internus, leads to an increased delay of the slower component. On the contrary, the recordings obtained by moving the electrode perpendicular to the bundle of fibers, at various depths, show only variation in form and amplitude. The diphasic potentials recorded do not originate from a double stimulation, due to the type of electrodes used. Actually, the stimulation by the cathode of the lateral ampullary nerve, with the anode placed on the ear muscles, does not bring about any modification of the form of the action potential. It has been, however, difficult to show a difference of the stimulation threshold for each component of this potential. This phenomenon could be due to the difference in diameter among the stimulated preganglionic fibers and the recorded postganglionic fibers.

Discussion

(A) Neurophysiological study

The experiment was carried out under sodium pentobarbital anaesthesia, and the depressive action of this drug upon the responses of the vestibular neurons has already been mentioned [17]. However, the length of the experimental procedure involved in our technique justifies the use of anaesthesia. Furthermore, since the recording was done quite some time after the beginning of the barbiturate anaesthesia, its depressive action was considerably reduced at the time of the experiment itself.

The study of the responses brought about in 147 cells deprived of spontaneous activity and distributed in the lateral medial and descending vestibular centers, has enabled us to reach various conclusions. First of all, the neuronal activities brought about by the stimulation of the vestibular nerve do not show any fundamental difference as a function of the cellular distribution inside the

vestibular complex. There is not any important functional and neuroanatomical functional difference between the vestibular centers or their subdivisions.

(I) Analytical study of the responses considered as a whole

(a) The latencies of the first spikes are divided into two groups: 0.8 - 1.1 msec; 1.1 - 1.6 msec. The monosynaptic nature of the first group, as proposed by Precht and Shimazu [17], was demonstrated on the basis of intracellular recordings done by Ito et al. [10]. As to the responses of the second group, the latter authors have estimated that all the cells recorded in the medial portion of the lateral vestibular center were disynaptic. This opinion was based in the impossibility of showing a difference of the threshold of stimulation between the responses of each of the two groups. This hypothesis appeared possible, considering the fact that the existence of interneurons in the medial and descending centers has been proposed [9 - 12], whereas their absence is probable in the lateral vestibular center [16]. /349

However, the results of our structural and functional study of the vestibular nerve is prompting us to consider some of the responses characterized by a long latency (type 2) as being monosynaptic. The detailed argumentation of this point will be given in the third part of this discussion.

(b) A second spike appeared in 38% of the cases. Precht and Shimazu [17] have described similar responses in some neurons following intense stimulation. In the present work, this type of response has been encountered in the three vestibular centers under study, for cells which do not have any spontaneous activity, and at the time of slight preliminary stimulations. This second spike is the expression of either a repetitive discharge or of the arrival of an impulse which has traveled through intranuclear neurons or other intranuclear or cerebral circuits.

(c) A certain number of cells responds to stimulation with several spikes. These repetitive spikes appear at regular intervals, and are originated by weak stimulation. We could be dealing, as was suggested by Ito et al. [10], with monosynaptic activities caused by a series of impulses derived from the stimulation of vestibular receptors.

(II) Characteristics of the responses as function of the method of stimulation

Following heat stimulation in the guinea pig, Desole and Pallestrini [5] have shown that the great majority of the vestibular neurons with spontaneous activity are influenced by the stimulation of two or more labyrinth receptors. A less pronounced convergency as been reported by Curthoys and Markham [4] in the cat. In our recordings, we have found that, following electric stimulation, only some of the impulse was converging on the same cell. The use of pentobarbital as aneesthetic, as well as the difficulty of stimulating selectively and successively all of the vestibular branches in the same animal, could undoubtedly suggest some reserve in this connection. The infrequency of convergence phenomena seems, however, a reality. It has already been mentioned by Wilson and Felpel [22], during the electric stimulation of the semi-circular canals in the pigeon, and by Kasahara and Uchino [11] — in the cat. The different results obtained by the authors, using either heat or rotatory stimulation, are due, perhaps, to different cellular modes of reaction.

Our results suggest also a specificity of the vestibular neurons for a certain type of stimulation. There seems to be, in fact, on each neuron a projection of preference for a specific receptor, the influence of which would manifest itself as a repetitive discharge, whereas the stimulation of another receptor would be, in most cases, without effect. As to the neurons receiving converging impulses, 350
they would exhibit a different synaptic arrangement, depending on the receptor which has been stimulated. To better define these interrelationships, it is necessary to conduct an intracellular study.

The relationships existing between the diameter of the fibers and the latencies of the responses in the centers will be discussed further.

(III) Topographic characteristics of the responses

(a) Lateral vestibular center. It is characterized by the massive projection of the utricle, and by its density in the lateral regions of transition between the dorsal and ventral portions. Lorente de Nó [12] has already demonstrated in the mouse the importance of this projection in the center. Gacek [8] has described the convergence of a considerable number of utricular fibers in the lateral regions. The ampullary receptors project themselves in the ventro-medial regions. It is particularly remarkable that we encountered only very little response in the dorsal portion of the center. Walberg et al. [19] had already noticed that the primary vestibular projections in the cat are strictly localized in the ventral portions. Furthermore, the route taken by the vestibular impulses, directed toward the dorsal region, remains hypothetical [2]. However, the high infrequency of the responses, even of those characterized by a long latency, can be explained either by the action of pentobarbital upon complex polysynaptic circuits, or by the fact that we have eliminated from our recordings the spontaneous activities which are one of the characteristics of the dorsal neurons [23].

(b) Medial vestibular center. The labyrinthic projections have been studied particularly by Wilson et al. [24]. According to these authors, 22% of the monosynaptic responses originate from cells located in the rostral portion, while the polysynaptic responses (33%) originate from the neurons which are uniformly distributed, but which in 73% of the cases exhibit a spontaneous activity. This characteristic explains the fact that we noticed practically no polysnyaptic response. The neurons we recorded exhibit the same characteristics as the other centers, but with very few responses having a latency higher than 1.1 msec. This result, according to our hypothesis, would seem to point to a preferential projection of the ampullary cristae on the medial vertibular center, and this is in agreement with the majority of the histological findings [8, 12, 18].

There is, however, a not insignificant projection of the utricle on the rostral portion of the medial vestibular center. It is actually difficult to estimate its importance, due to the absence of a sufficient number of combined stimulations of the utricle-ampullary cristae. This projection is unquestionable, and corresponds to the one recently described from the anatomical point of view in the cat by Gacek [8]. It could modify in part the concept of the role played by the medial vestibular center. In fact, Nyberg-Hansen [15] has well shown the projection of the medial center on the cervical marrow through the intervention of the descending medial longitudinal fasciculus. This fact was confirmed by Wilson et al. [24]. It would be interesting to know if these utricular projections have synaptic contacts with the neurons having their axons at the origin of the medial vestibulo-spinal fasciculus, while the conduction of the majority of the impulses with tonic termination, remains the property of the lateral vestibulo-spinal fasciculus originating from the lateral center.

(c) Descending center. The vestibular projections of mono- /351
synaptic type are limited to its rostral portion in the cellular region, where the fibers are not yet organized in a longitudinal direction. In it, the projections of the utricle and of the semicircular canals are closely mixed, and the proportion of the double responses reaches 50%, as in the medial vestibular center, while it is only 26% in the lateral center. This finding is undoubtedly related to the distinct role of each center in the regulation of tone and posture with the descending center being a link in the cerebellar cerebello-vestibulo system [3].

(B) Histological and Physiological Study of the Vestibular Nerve

(1) The results of our histological studies show that the vestibular nerve contains fibers with a significantly different diameter. If McFarland and Friede [13], following planimetric measurements in the cat, found that the diameters of the fibers of the

stato-acoustic nerve had a unimodal distribution, this result cannot be opposite to ours. In effect, the cochlear fibers, more numerous and finer than the vestibular fibers, give a very particular aspect to the histogram of the eighth pair, considered as a whole. Engström and Rexed [7] have already pointed out that in man the spectrum of the fibers is very narrow in the cochlear nerve region, while it is much more diffuse in the vestibular nerve. The physiological investigation we performed confirms, on the other hand, the presence in the vestibular nerve of fibers with a different speed of conduction.

(2) The rostral and caudal portions of the vestibular nerve contain, respectively, the nerves of the ampullary cristae and the nerves of the utricular and saccular maculae. This fact, already established by Gacek [8], was confirmed with out longitudinal sections. The statistical analysis of our data allow us to state that the fibers originating from the semicircular canals are thicker than the fibers originating from the utricle and the sacculus.

(C) Anatomofunctional Correlations

The responses obtained in the vestibular centers exhibit latencies varying between 0.8 and 2 msec. This wide gamma of values indicates, perhaps, for the longer responses, the presence of an interneuron, if one admits the existence of only one type of fiber in the vestibular nerve. In effect, the measurement of the diameters of the postganglionic fibers shows with certitude that their spectrum varies at least between 1.2 and 10.2 µm. This point is in agreement with other results. Hauglie-Hanssen [9], in his study on the organization of the nuclear vestibular complex, encounters great differences in the diameter of the fibers of the intracerebral portion of the vestibular nerve. Mugnaini et al. [14] had previously pointed out that, after cutting of the vestibular nerve, all the terminal buttons do not degenerate at the same speed. This fact can be explained on the basis of the difference of thickness of the fibers at the end of which they are located. Having established the fact of different diameters for the fibers, this implies very different responses in

cellular latencies for the vestibular centers. The absence in our study of antidromic stimulations, concerning, among other parts, the /352
spinal cord, the cerebellum, and the medial longitudinal fasciculus, does not allow us to state that some of the recorded neurons were not intercalary neurons. This fact makes it impossible to exclude the possibility of a supplemental synapsis. It seems, however, that a great number of responses with long latency have a monosynaptic origin. This hypothesis is supported by the establishment of correlations between these responses and the very thin fibers, considering the existence of a direct relationship between the speed of conduction of the nerve impulses and the diameter of the fibers. In effect, following utricular stimulation, 39% of the responses have more than 1.1 msec latency, while only 26% of them reach this value following ampullary stimulation. On the other hand, the histograms of the diameter of the fibers in the caudal and rostral portion of the vestibular nerve show that 39% and 23%, respectively, of the utricular and ampullary postganglionic fibers have a diameter of less than 3.7 μm. There is, therefore, a good correlation between the percentages of the responses with long latency (> 1.1 msec) and those of the thinnest fibers. These arguments are in favor of a monosynaptic origin for some of these responses, and for a larger number of thin postganglionic fibers originating from the utricular receptors, as compared to the ampullary receptors.

Wersäll [20] has shown the presence in the cristae and maculae of sensory cells of type I and II, supplied by fibers of large and small diameter. Type I cells were found to be more numerous in the ampullary cristae than in the utricular and saccular maculae.

From the results we obtained, it appears that this is a characteristic of the vestibular nerve, and it is perhaps related to the preferential projection of some receptors of the vestibular centers: the utricle in the lateral vestibular center, the semicircular canals in the medial center.

It is, therefore, possible to conclude that there is a selective direct projection on the neurons of the primary centers of the different fibers having preferred relationships with the sensory cells of type I or II, of the vestibular receptors, according to their diameter.

Summary

By means of electrical stimulation of the nerve fibers originating in the cristae ampullares and the utricle, it was possible to test the reactivity of a certain number of neurons devoid of spontaneous activity, in the lateral, median, and descending vestibular nuclei of the cat.

(1) Two groups of responses are discernible: the first, said to be type 1, of very short latency (0.9 msec); the second, said to be type 2, of longer latency (1.3 msec). In each group there exist single and double responses; in the latter case, the second spike occurs 0.8 msec after the first.

(2) Few neurons receive direct impulses from different receptors simultaneously. The majority respond preferentially to one particular category.

(3) Responses differ according to the receptors involved. Thus, the latencies of the first spikes are longer after utricular stimulation than after ampullar stimulation. /353

(4) The responses tend to take on a specific character, depending on which of the three vestibular nuclei is under consideration. In the lateral nucleus, in particular, the vestibulotopy is relatively marked, and the utricular projections are greater than in the descending and median vestibular nuclei.

(5) A histological study of the structure of the vestibular nerve shows that the postganglionic fibers of ampullar and utricular

origin vary in diameter. Furthermore, the ampullar fibers are thicker than the utricular fibers. These differences in diameter are confirmed by recordings of the activity transmitted by these fibers.

(6) Various structural and physiological relationships emerge from these results. For example, a partial examination of the differences in latency between the two groups of responses in the vestibular nuclei is to be found in the varied diameters of the fibers transmitting the impulses. Other correlations concern the topographic specificity of the projections in the nuclei and the distribution of the fibers according to their origins.

Acknowledgements

This work was carried out with the support of the C.N.R.S. and the I.N.S.E.R.M., with the collaboration of P. Massal, P. Sibleyras, and J. Boyer.

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Translated for National Aeronautics and Space Administration under contract No. NASw 2483, by SCITRAN, P. O. Box 5456, Santa Barbara, California, 93108